

## VASCULAR AND NON-VASCULAR PLANT COMMUNITY RESPONSE TO SILVICULTURAL PRACTICES AND RESULTANT MICROTOPOGRAPHY CREATION IN A FORESTED WETLAND

Heidi M. Anderson<sup>1,3</sup>, Margaret R. Gale<sup>1</sup>, Martin F. Jurgensen<sup>1</sup>, and Carl C. Trettin<sup>2</sup>

<sup>1</sup>*School of Forest Resources and Environmental Science*

*1400 Townsend Dr.*

*Michigan Technological University  
Houghton, Michigan, USA 49931-1295*

<sup>2</sup>*Center for Forested Wetlands Research  
Southeastern Forest Experimental Station*

*2730 Savannah Highway  
Charleston, South Carolina, USA 29414*

<sup>3</sup>*Current address:*

*P.O. Box 568*

*Gardiner, Montana, USA 59030*

*E-mail: Heidi\_Anderson@nps.gov*

**Abstract:** Forested wetlands are important ecosystems valued for their indigenous plant communities, spatial heterogeneity, wildlife habitat, water quality, and timber resources. When harvested for timber, plant composition in these wetlands may change due to alteration in microsite habitats. Harvest severity also may affect plant composition. In this study, a mineral conifer wetland was subjected to whole-tree harvesting followed by installing different site preparations (bedding, trenching, draining). The original wetland overstory was *Picea mariana*, *Larix laricina*, and *Pinus banksiana*, with groundcover dominated by *Sphagnum russowii*. Eleven to twelve years after harvest, we assessed responses of vascular and non-vascular plants to created microtopographies (pits, side slopes, mounds) to determine whether harvest severity affected species richness, diversity, and relative cover of plant communities. For all the microtopography positions, the more severe harvest treatments (drained, cut, trenched) had the highest plant richness but the lowest diversity values. Richness and relative cover of *Sphagnum* species were highest in reference areas and much lower in the most severe harvest treatments (drained, cut, trenched). In contrast, graminoid and, to a lesser extent, herbaceous and woody plants increased in richness and cover after harvest.

**Key Words:** bryophytes, drainage ditches, microtopography, site preparation, *Sphagnum*, timber harvest

### INTRODUCTION

Forested wetlands provide important ecosystem functions and values including aesthetics, biotic diversity, indigenous plant communities, spatial heterogeneity, wildlife habitat, water quality, and timber resources. The occurrence of pit and mound microsites is an important ecological component within forested wetlands. Wind disturbance, one of the most common types of small-scale natural disturbance (Bray 1956, Runkle 1981, Brokaw 1985, Schaetzl et al. 1989b, Peterson and Campbell 1993), can create natural pit and mound microtopography in shallow rooted ecosystems (Stone 1975, Beatty and Stone 1986, Schaetzl et al. 1989a, 1990, Liechty et al. 1997). These features can persist on the

landscape for 200 to 2,000 years (Beatty and Stone 1986, Schaetzl and Follmer 1990, Liechty et al. 1997). These microsites, in conjunction with the hydrology of forested wetlands, have been found to maintain diversity of woody plants (Chimner and Hart 1996, Roy et al. 1999) and bryophytes in boreal forest ecosystems (Jonsson and Esseen 1990, Palisaar and Poschod 2001). However, less is known about how man-made disturbances such as harvesting and site preparations affect wetland plant communities.

Harvesting alone significantly affects plant diversity by altering the microclimate, reducing the quantity of suitable substrate, and fragmenting large forest areas (Söderström 1988, Andersson and Hytteborn 1991, Lesica et al. 1991, Palisaar and

Poschlod 2001). Microsites created by harvesting and subsequent site preparation may physically mimic natural pit and mound microtopography and could offer a way to mitigate the effects of harvesting on plant communities. Natural pit and mound sites in forested wetlands can vary from old decayed logs to windthrown root plates; human created microsites may be less variable. Although disturbance can maintain natural communities (Sousa 1984), knowledge of the degree, scale, and frequency of disturbance is important (Levin and Paine 1974, Osman 1977, Connell 1978, Denslow 1980, Miller 1982). Harvesting produces patches much larger than those created by natural windthrow (Sousa 1984) and therefore issues of scale and degree may be important.

Although site preparation can enhance tree regeneration in wetlands, these techniques also affect regeneration of other vegetation (Gale *et al.* 1998). Without a better understanding of the degree to which harvesting and site preparation imitate natural windthrow disturbance, and how plant communities rebound from mechanical disturbance, it is difficult to know the extent to which these ecosystems are being altered. Site preparation techniques may accelerate succession and eliminate certain plant species, particularly bryophyte species that recover slowly from disturbance (Hunter 1990, Haeussler *et al.* 1999).

Plant communities in the understory are typically richer in biotic diversity than in the overstory (Raunkiaer 1934, Crawley 1986, Halpern and Spies 1995, Thomas *et al.* 1999), and non-vascular plants are especially sensitive to forest management (Berg *et al.* 1994, Haeussler *et al.* 1999). Few studies have considered how site preparation techniques designed to enhance tree growth might come at the expense of a less rich plant community, more invasive species, decreased bryophyte cover, and a functionally diminished wetland. With more public interest in sustainable forestry and wetland protection, a closer examination of the relative effects of human-created microsites on plant communities compared to natural windthrown microsites could produce valuable information on whether silvicultural practices can mimic natural processes.

The goal of this study was to examine recovery of vascular and non-vascular plant communities 11 to 12 years after draining, harvesting, and site preparation (trenching, bedding) in a forested mineral wetland of Michigan's Upper Peninsula. The questions posed were: 1) Does plant diversity and composition differ across man-made pit and mound microsites when compared to natural ecosystems?

and 2) Do pit and mound plant communities differ with the severity of site preparations?

## METHODS

### Site Description

The study wetland was located near Munising in Alger County in the Upper Peninsula of Michigan, at approximately 46°9'30" N latitude and 80°41'30" E longitude (Figure 1). The climate is continental with a mean annual total precipitation of 840 mm, approximately 40% of which is snow (Albert *et al.* 1986). The average growing season is 114 days with an average temperature of 14.4°C. The histic-mineral wetland had a Typic Haplaquod, sandy, mixed, frigid Kinross soil underlain by Ordovician/Trenton Limestone (Trettin *et al.* 1992), and was part of the Wetmore outwash plain. High water tables are due to heavy snow melt during the spring and copious amounts of rainfall during the fall. Pre-experiment overstory vegetation was a 60-year-old mixed conifer stand consisting of black spruce (*Picea mariana* (Mill.) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch), and jack pine (*Pinus banksiana* Lamb.). Dominant species in the shrub layer were blueberry (*Vaccinium angustifolium* (Ait.) Gray and *V. myrtilloides* Michx.), leatherleaf (*Chamaedaphne calyculata* (L.) Moench.), and Labrador tea (*Ledum groenlandicum* Oeder.). The soil surface was almost entirely vegetated by *Sphagnum russowii* Warnst, with *Pleurozium schreberi* Brid (Mitt) and *Dicranum polysetum* Sw. also contributing to the non-vascular plant element.

### Experimental Design

The study area was divided into four areas (Figure 1). The lower portion of the site had two 3-m wide drainage ditches installed in 1984, while the upper portion remained undrained. In 1988, approximately half of the drained and undrained areas were then clearcut using a mechanized whole-tree harvesting system. Eight treatments within these four portions of the wetland were developed.

**Treatment 1.** The area that remained undrained and uncut served as the intact *reference treatment* for the study. Microtopographies within this area included pits, side slopes, and mounds. Pits were depressions and mounds were hummocks. A side slope was the transitional slope between a pit and a mound.

**Treatments 2, 3, and 4.** Three treatments were developed in the undrained, cut area. One treatment

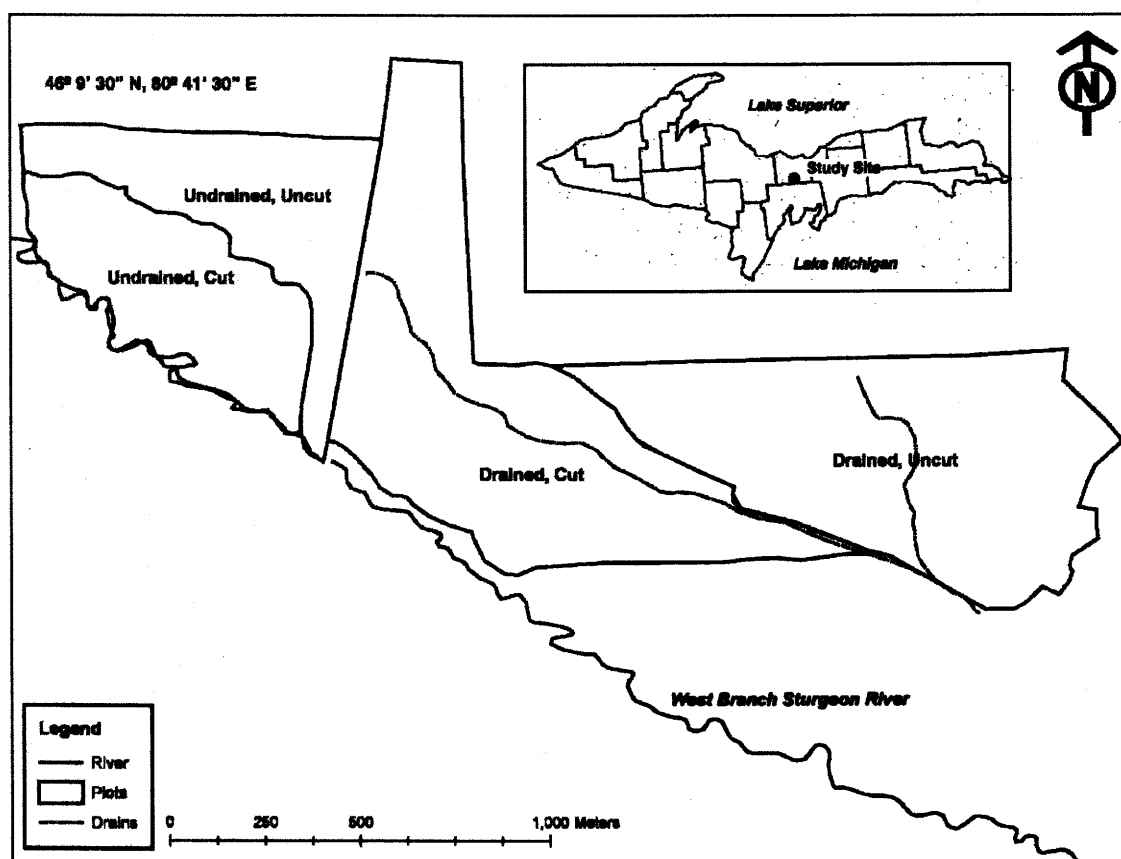


Figure 1. Map of the study area in relation to the West Branch of the Sturgeon River, Michigan.

was not manipulated further and was designated as a *harvest-only treatment*. Microtopography existing in this treatment was natural, and was classified as in the reference treatment.

The second treatment was trenched using a TTS disc trencher, which disturbed approximately 45% of the soil surface (Trettin et al. 1997). This *undrained, cut, and trenched treatment* had created microtopographies. The 20-cm deep trenches themselves were considered analogous to depressional pits. Berms (Figure 2A) were composed of forest floor and mineral soil material displaced from the trenches and were the mound microsites in this treatment. Side slopes were transitional between trenches and berms.

A third treatment was bedded by disking the soil into elevated planting beds using an Eden Relief Bedding Plow that tilled the entire soil surface (Trettin et al. 1997). A mixture of forest floor and mineral soil was disked into elevated planting beds (Figure 2B). In this *undrained, cut, bedded treatment*, beds were considered mounds, depressions next to the beds were considered pits, and side slopes were the transitions between beds and pits.

**Treatments 5 and 6.** In the drained, uncut area, two treatments were developed to assess how proximity to the drainage ditch affected plant communities. Plots were selected along transects located 30 m and 120 m from the drainage ditch (four plots at each distance). In both the *30-m, drained, uncut treatment* and the *120-m, drained, uncut treatment*, microtopography was from natural pits, mounds, and side slopes.

**Treatments 7 and 8.** In the drained, cut area, a 25-ha area was prepared using a TTS disc trencher. As above, the plots were selected along transects 30 and 120 m from the drainage ditch. In the *30-m drained, cut, trenched treatment* and the *120-m drained, cut, trenched treatment*, trenches were pits, berms were mounds, and side slopes the areas between trenches and berms.

All cut areas were planted with jack pine seedlings (1-0) in late summer 1988 after site preparation treatments were complete. In the harvest-only treatment, trees were planted on the natural soil surface at 2-m spacing. In the trench treatments, trees were planted on the upper shoulder of the

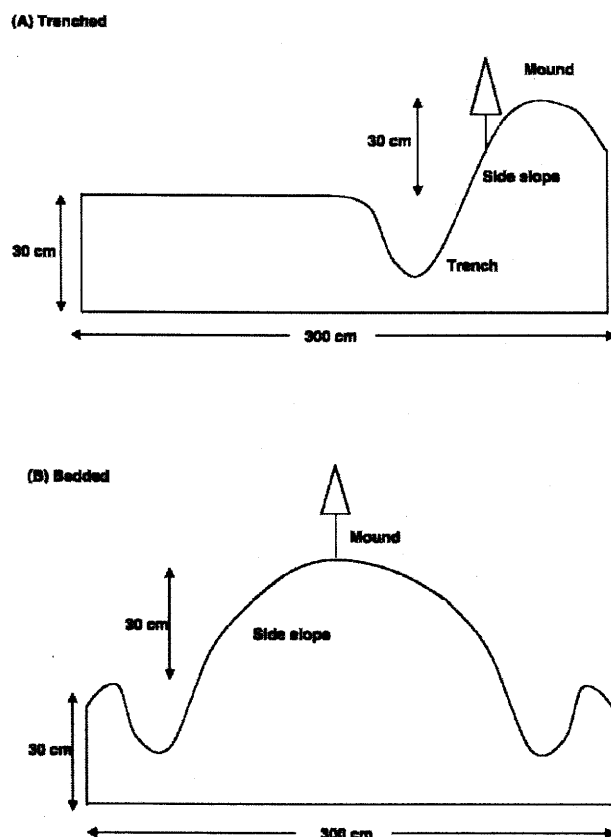


Figure 2. Profile views of created microtopographies (mound, side slope, and pit) for the A) trench site preparation treatment and B) bedded site preparation treatment.

trench at 2-m spacing. In the bedded treatment, seedlings were planted in the center of elevated beds, with one to three seedlings per bed.

The eight treatments developed in this study included a broad range in the severity of disturbance, and qualitatively could be ordered from least to most severe as follows: 1) reference; 2) 120-m drained, uncut; 3) 30-m drained, uncut; 4) harvest-only; 5) undrained, cut, trenched; 6) undrained, cut, bedded; 7) 120-m drained, cut, trenched; and 8) 30-m drained, cut, trenched. Treatments 7 and 8 each had three manipulations, Treatments 5 and 6 each had two manipulations, Treatments 2, 3, and 4 each had one manipulation, and Treatment 1 was unmanipulated.

#### Vegetation Sampling

Our sampling was conducted in 1999 and 2000, which was 11–12 years after the initial harvests were conducted. In each of the eight treatments, we selected four 32 × 32 m sample plots. Within each

plot, we selected five 1,000 cm<sup>2</sup> subplots spaced at 5-m intervals along diagonal transects across the plots, starting 10 m from the southeast corner of each plot. Within each subplot, we sampled three adjacent microsite positions (pit, mound, and side slope) (3 microsites × 5 subplots × 4 plots = 60 samples per treatment). Only understory plants (<1 m) were censused, including the presence of any planted jack pine. In each microplot, vascular and non-vascular plant composition and cover were recorded. Occasionally, a species lacked the sporophyte or flowering structure necessary for species identification, and those plants were categorized to genus only. Two people visually assessed cover values for each plant species, with cover being defined as “an estimate of the area of coverage of the foliage of the species in a vertical projection onto the ground” (Shimwell 1971, Hellquist and Crow 1999). Cover values from the two people were averaged. Species with less than 1% cover were assigned a value of 0.5. Nomenclature followed Gleason and Cronquist (1991) for vascular plants, Crum and Anderson (1981) for mosses, and Crum (1991) for liverworts. Lichens and leafy liverworts were not identified to genus or species, but classified as morpho-species of non-vascular species.

#### Analysis

Because treatments were not replicated, statistical contrasts among treatments were not conducted. However, we calculated various descriptive statistics for each treatment. We estimated means and standard errors for each microtopography within a treatment, and pooled data from all microsites to describe an overall treatment means and error. We estimated total species richness and calculated Simpson's diversity index where  $D_s = 1 - \sum (n_i - 1) / (N(N - 1))$ . We calculated relative cover for each plant species, but also pooled species into herbaceous, graminoid, woody, and non-vascular plant categories and calculated relative cover of these groups. Because of the importance of *Sphagnum*, we kept that genus as its own category.

## RESULTS

#### Plant Richness, Diversity, and Occurrence

We identified 52 vascular plant species (Appendix); of which 25 were woody, 20 were herbaceous, and seven were graminoid species. Herbaceous and graminoid richness was greatest in 30-m and 120-m drained, cut, and trenched treatments (Table 1), which were the two most severely disturbed treat-

Table 1. Total bryophyte, *Sphagnum*, non-*Sphagnum* bryophyte, total herbaceous, graminoid only, non-graminoid herbaceous, and woody species richness for the eight treatments.

	Reference	120-m Uncut	30-m Uncut	Harvested	Bedded	Trenched	120-m Trenched Cut	30-m Trenched Cut
Bryophytes	25	17	26	18	20	18	24	20
<i>Sphagnum</i>	12	8	10	7	6	7	8	7
Non- <i>Sphagnum</i>	13	9	16	11	14	11	16	13
Herbaceous plants	8	7	6	10	12	11	21	21
Graminoids	3	3	2	4	3	3	6	5
Others	5	4	4	6	9	8	15	16
Woody plants	14	15	11	11	12	7	14	18
Total species	47	39	43	39	44	36	59	59

ments. The 30-m drained, cut, and trenched treatment also had the highest woody species richness with 18 species (Table 1).

We identified 50 bryophyte species, 18 of which were *Sphagnum* (Appendix). Bryophyte richness was greatest in reference (25 species), 30-m drain, uncut (26 species), and the 120-m drain, cut, and trenched (24 species) treatments (Table 1). The reference treatment had the highest *Sphagnum* richness with 12 species (Table 1). *Sphagnum* species richness differed somewhat among microsites. Average richness was highest on the side slopes (1.04 species), compared to the pit (0.95) and mound (0.76) microsites.

Simpson's diversity index ranged from a high of 0.717 in the harvest-only treatment to a low of 0.589 in the most severely impacted 30-m, cut, trenched treatment (Figure 3). Side slope ( $D_s = 0.683$ ) and mound ( $D_s = 0.662$ ) microsites were more diverse than pit microsites ( $D_s = 0.590$ ).

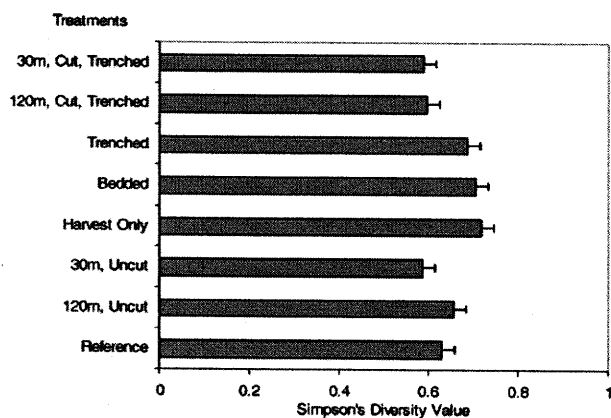


Figure 3. Average Simpson's diversity values ( $\pm$  standard error) for all plant species on mound, side slope and pit microsites in eight site preparation treatments.

Of the herbaceous species, *Coptis trifolia* (L.) Salisb. and *Maianthemum canadense* Desf. occurred in every treatment and almost all microsites (Appendix). *Deschampsia flexuosa* (L.) Muhl. and *Rubus hispidus* L. had high relative cover in most cut treatments (Appendix). Of the woody species, *Vaccinium myrtilloides*, *V. angustifolium*, *C. calyculata*, and *Gaultheria procumbens* L. occurred in all treatments and microsites (Appendix). *Vaccinium* cover tended to be lower in high severity disturbance treatments, with *V. myrtilloides* cover being particularly sparse in 30-m drained, cut, trenched treatment. Seven species (*Amelanchier stolonifera* Wiegand, *Lonicera villosa* (Michx.) Schult., *P. banksiana* Lambert, *Picea glauca* (Moench) Voss, *Populus tremuloides* Michx., *Spiraea alba* Duroi, and *Salix* sp.) occurred in only a single treatment each, but four of these (*A. stolonifera*, *P. banksiana*, *P. tremuloides*, and *S. alba*) occurred in treatments with high severity disturbance.

Of the non-vascular plants, *Sphagnum russowii* occurred in all treatments, although it was absent from some microsites in the drained, cut, and trenched treatments (Appendix). *Aulacomnium palustre* (Hedw.) P.-Beauv. and *D. polysetum* were also fairly ubiquitous on all treatments. *Polytrichum commune* Hedw. occurrence was greater on the harvested than the uncut treatments. Eight species (*Atrichum undulatum* (Hedw.) P.-Beauv., *Brachythecium* sp., *Ceratodon purpureus* (Hedw.) Brid, *Hypnum lindbergii* Mitt., moss sp. 2, *Pellia* sp., *Plagiothecium denticulatum* (Hedw.) Schimp. in B.S.G., and *Sanionia uncinata* (Hedw.) Loeske) were only found once, four of which (*H. lindbergii*, moss sp. 2, *P. denticulatum*, and *S. uncinata*) were found in the uncut treatments. Another nine species (*Bryum* spp., *Hylocomium splendens* (Hedw.) BSG, moss sp. 3, *Plagiommium* spp., *Sphagnum angustifo-*

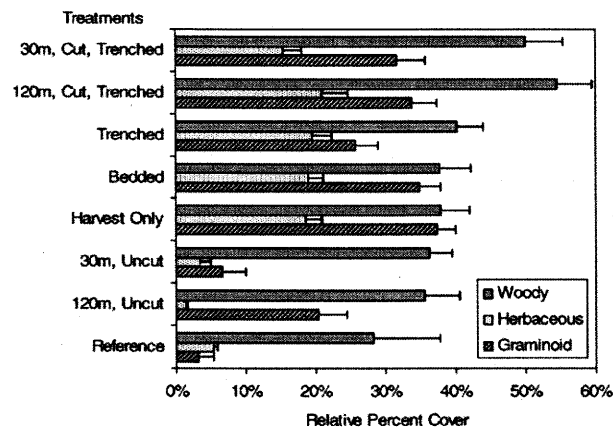


Figure 4. Average relative cover ( $\pm$  standard error) of graminoid, other herbaceous, and woody plants on mound, side slope, and pit microsites in eight site preparation treatments.

*lium* (C. Jens. Ex Russ.) C. Jens in Tolf., *Sphagnum recurvum* P.-Beauv., *Sphagnum subsecundum* Nees in Sturm, *Sphagnum nitidum* Warnst., and *Tetraphis pellucida* Hedw.) occurred exclusively in the uncut treatments (Appendix).

#### Relative Cover

Graminoid relative cover was greatest in the harvest-only treatment (37%; Figure 4), and was low in the reference and the 30-m drained, uncut treatments. Graminoid relative cover was highest in pits for all treatments except the harvest-only and 120-m drained, uncut treatments where graminoid relative cover was highest on side slopes. Herbaceous relative cover was low in uncut treatments and high in harvested treatments (Figure 4). Cover of woody species was relatively high in all treatments, and especially so in the 30-m and 120-m drained, cut, trenched treatments (Figure 4). In cut treatments, woody cover was high on mounds (63%) and low in pits (21%), while in uncut treatments, woody cover was similar among microsites.

*Sphagnum* cover declined steadily as disturbance severity increased, with cover ranging from 71% in the reference treatment to 8%–9% in the two drained, cut and trenched treatments (Figure 5). Of the treatments where timber was harvested, the harvest-only treatment retained the greatest *Sphagnum* cover (40%; Figure 5). In uncut treatments, pit and side slope microsites tended to have the highest *Sphagnum* relative cover, and surprisingly the same pattern existed for the drained, cut, and trenched treatments (albeit at much lower levels). In contrast, in the harvest-only treatment, *Sphagnum* cover was greatest on mounds (Figure 5).

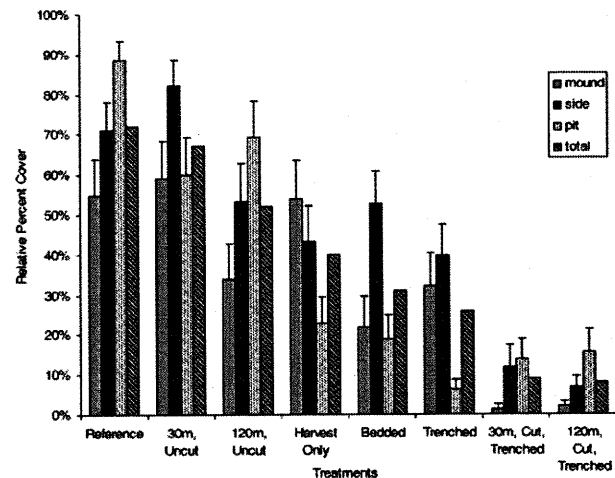


Figure 5. Average relative cover ( $\pm$  standard error) of *Sphagnum* bryophyte species on mound, side slope, and pit microsites in eight site preparation treatments.

Unlike *Sphagnum*, cover of other bryophytes tended to increase with disturbance severity, ranging from 80% relative cover in the 120-m, cut, trenched treatment to 26% in the reference (Figure 6). In general, treatments with the lowest *Sphagnum* relative cover had the highest non-*Sphagnum* cover and vice versa (Figures 5 and 6). In terms of microsite use, in the three uncut treatments, cover of *Sphagnum* and non-*Sphagnum* bryophytes tended to be negatively associated (e.g., on mounds, *Sphagnum* cover was relatively low while non-*Sphagnum* moss cover was relatively high; Figures 5 and 6).

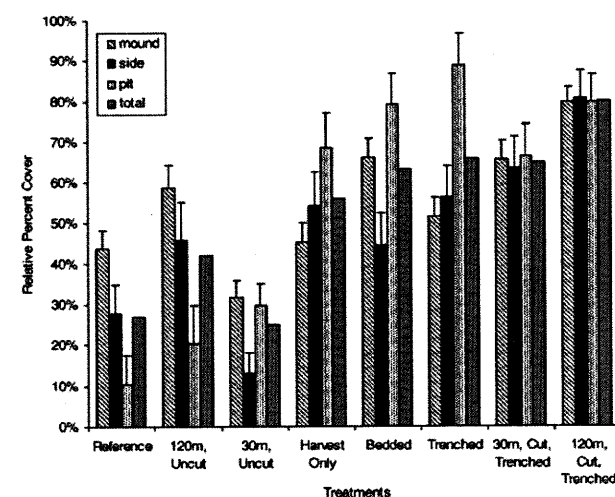


Figure 6. Average relative cover ( $\pm$  standard error) of non-*Sphagnum* bryophyte species on mound, side slope, and pit microsites in eight site preparation treatments.

## DISCUSSION

The most dramatic finding to emerge from this study was the virtual lack of *Sphagnum* cover on drained, cut, and trenched treatments (Figure 5, Appendix). Drainage by itself had relatively little impact on *Sphagnum*. Among the five harvested treatments, the harvest-only treatment was most similar to the reference treatment in terms of *Sphagnum* richness and relative cover. The mound microsites in the harvest-only treatment had six species of *Sphagnum*, while the remaining harvested treatments had at most two species, suggesting that harvest by itself had less impact on species richness than site preparation. However, the reference treatment had 12 *Sphagnum* species indicating that harvest still had long-term impacts.

The negative response of *Sphagnum* to mechanical site preparation suggests that intensity of disturbance may play crucial roles in *Sphagnum* survival and colonization. In another study at our research site, Trettin et al. (1997) found that organic matter decomposition rates increased after disturbance, with the greatest decomposition rates occurring in the bedded area, followed by the trenched area. Rapid decomposition might negatively affect *Sphagnum* recovery. Variation in *Sphagnum* relative cover may also be related to tree occupancy. Tree occupancy in the bedded areas was higher than in trenched areas (Gale et al. 1998), and because of a more closed canopy and more humid microenvironment, bedding may enhance *Sphagnum* recovery over trenching. We also found that *P. schreberi* cover was much lower in harvested than non-harvested treatments. In other studies, mortality of this plant was correlated with higher temperatures (During and Van Tooren 1990), and a lack of shading may have inhibited *P. schreberi*.

A second pattern of interest was the opposite response of *Sphagnum* and non-*Sphagnum* bryophytes. Site drying from draining, harvesting, and trenching may harm *Sphagnum*, but other bryophytes can apparently colonize the dry, disturbed soil. During (1979) and Laine et al. (1995) suggested that drainage permits bryophytes usually restricted to drier hummocks to spread.

Graminoid, herbaceous, and woody plant cover generally increased with disturbance, which corresponds to results in uplands (Haeussler et al. 1999). However, negative impacts of disturbance tend to be of more concern than positive impacts, and thus *Sphagnum* might be the superior bioindicator of environmental change in wetland ecosystems, even those with mineral soils such as the study site.

In this study, we were particularly interested in the effects of microtopography. Site preparation may affect plant communities because the disturbance severity and the microtopographies created can both vary dramatically. High *Sphagnum* and bryophyte richness on natural microtopography in this study agrees with Palisaar and Poschlod (2001) who also found high *Sphagnum* and bryophyte species numbers and abundance on natural windthrow microtopographies of montane forest in Germany. Although creating microsites may provide niches for different species and with time bryophyte cover and richness may gradually increase in our study sites, created sub-habitats may never duplicate ecological communities to natural systems (Gale et al. 1998, Haeussler et al. 1999).

However, in some harvested areas, creation of side slopes produced relatively high *Sphagnum* cover, perhaps because the environment of side slopes was more moderate than either mounds or pits. In addition, when all plant species were considered, side slopes had relatively high Simpson's diversity values, indicating these microsites may be important to overall heterogeneity of the floral communities. Aspects of microsite may have also contributed to other patterns of *Sphagnum* richness and cover in this study. Differences in the prevalence of *Sphagnum* in pits of drained and undrained tracts may be related to hydrology. Price and Whitehead (2001) found low *Sphagnum* recolonization (10%) on a block-cut peatland in Quebec 30 years after abandonment, where almost all of the *Sphagnum* recolonization was in trenches of the drains. Microsite features may also affect other plants. *Hylocomium splendens*, *P. denticulatum*, and *T. pellucida* were bryophytes found only in uncut treatments. These species are typically found on old log microsites, and harvested treatments may not provide sufficient large, coarse, woody debris for them. Several studies have suggested that bryophytes in managed forests decline from lack of substrate diversity (Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991, Vellak and Paal 1999). MacLean and Wein (1977) also found that bryophytes increase as stands age.

## ACKNOWLEDGMENTS

We thank Janice Glime and Kurt Pregitzer for comments on early versions on this paper. Assistance in identification of bryophyte and other plant species from Deb Anderson, Tim Barber, Greg Kudray, and Stephanie Stapleton was very helpful.

Mead-Westvaco Paper Company generously provided access to the study site and in-kind assistance. The National Council for Air and Stream Improvements and the McIntire-Stennis program provided funding for this project.

### LITERATURE CITED

- Albert, D. A., S. R. Denton, and B. V. Barnes. 1986. Regional landscape ecosystems of Michigan. School of Natural Research, Ann Arbor, MI, USA.
- Andersson, L. I. and H. Hytteborn. 1991. Bryophytes and decaying wood — a comparison between managed and natural forest. *Holarctic Ecology* 14:121–30.
- Beatty, S. W. and E. L. Stone. 1986. The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* 16:539–48.
- Berg, A., B. Ehnstrom, L. Gustafsson, T. Hallingback, M. Jonsell, and J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8:718–31.
- Bray, W. L. 1956. Gap-phase replacement in a maple-basswood forest. *Ecology* 37:598–600.
- Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. p. 53–69. *In* T. A. Pickett and P. S. White (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL, USA.
- Chimner, R. A. and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan Upper Peninsula. *Canadian Journal of Forest Research* 26:389–93.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10.
- Crawley, M. J. 1986. The structure of plant communities. p. 1–50. *In* M. J. Crawley (ed.) *Plant Ecology*. Blackwell, London, UK.
- Crum, H. 1991. Liverworts and hornworts of southern Michigan. The University of Michigan Herbarium, Ann Arbor, MI, USA.
- Crum, H. A. and L. E. Anderson. 1981. Mosses of Eastern North America. Volumes 1 and 2. Columbia University Press, New York, NY, USA.
- Denslow, J. D. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18–21.
- During, H. J. 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia* 5:2–18.
- During, H. J. and B. F. Van Tooren. 1990. Bryophyte interactions with other plants. *Botanical Journal of the Linnean Society* 104:79–98.
- Gale, M. R., J. W. McLaughlin, M. F. Jurgensen, C. C. Trettin, T. Soelsepp, and P. O. Lydon. 1998. Plant community responses to harvesting and post-harvesting manipulations in a *Picea-Larix-Pinus* wetland with a mineral substrate. *Wetlands* 18:150–59.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, second edition. New York Botanical Garden, Bronx, NY, USA.
- Gustafsson, L. and T. Hallingbäck. 1988. Bryophyte flora and vegetation of managed and virgin coniferous forests in south-west Sweden. *Biological Conservation* 44:83–300.
- Haeussler, S., L. Bedford, J. O. Boeteng, and A. MacKinnon. 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. *Canadian Journal of Forest Research* 29:1084–1100.
- Halpern, C. B. and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5:913–34.
- Hellquist, C. E. and G. E. Crow. 1999. The distribution of the bryophytes and vascular plants within Little Dollar Lake peatland, Mackinac County, Michigan. *Rhodora* 101:46–86.
- Hunter, M. L. 1990. *Wildlife, Forests and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice Hall, Englewood Cliffs, NJ, USA.
- Jonsson, B. G. and P. A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *Journal of Ecology* 78:924–36.
- Laine, J., H. Vasander, and R. Laiho. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology* 32:785–802.
- Lesica, P., B. McCune, S. V. Cooper, and W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* 69:1745–55.
- Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation and community structure. *Proceedings of the National Academy of Science USA* 68:1246–48.
- Liechty, H. O., M. F. Jurgensen, G. D. Mroz, and M. R. Gale. 1997. Pit and mound topography and its influence on storage of carbon, nitrogen, and organic matter within an old-growth forest. *Canadian Journal of Forest Research* 27:1992–97.
- MacLean, D. A. and R. W. Wein. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. *Canadian Journal of Botany* 55:2818–31.
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *American Midland Naturalist* 4:533–36.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monograph* 47:37–63.
- Palisaar, J. and P. Poschod. 2001. Bryophyte diversity in cleared and uncleared windthrow gaps and the adjacent forest stands in the Bavarian Forest National Park, SE Germany. *Lindbergia* 26:46–54.
- Peterson, C. J. and J. E. Campbell. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. *Bulletin of Torrey Botanical Club* 4:451–60.
- Price, J. S. and G. S. Whitehead. 2001. Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. *Wetlands* 21:32–40.
- Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography*. Clarendon, Oxford, UK.
- Roy, V., P. Y. Bernier, A. P. Plamondon, and J. C. Ruel. 1999. Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. *Canadian Journal of Forest Research* 29:563–74.
- Runkle, J. R. 1981. Gap regeneration in some old growth forests of eastern United States. *Ecology* 62:1041–51.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1989b. Tree uprooting: review of impacts on ecology. *Vegetatio* 79:165–76.
- Schaetzl, R. J., D. L. Johnson, S. F. Burns, and T. W. Small. 1989a. Tree uprooting: review of terminology, process, and environmental implications. *Canadian Journal of Forest Research* 19:1–11.
- Schaetzl, R. J., S. F. Burns, T. W. Small, and D. L. Johnson. 1990. Tree uprooting: review of types and patterns of soil disturbance. *Physical Geology* 11:277–91.
- Schaetzl, R. J. and L. R. Follmer. 1990. Longevity of tree-throw microtopography: implications for mass wasting. *Geomorphology* 3:113–23.
- Shimwell, D. W. 1971. *The Description and Classification of Vegetation*. University of Washington Press, Seattle, WA, USA.
- Söderström, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. *Biological Conservation* 45:169–78.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecological Systematics* 15:353–91.
- Stone, E. L. 1975. Windthrow influences on spatial heterogeneity in a forest soil. *Eidgenössische Anstalt für das forstliche Versuchswesen Mitteilungen* 51:77–87.



- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecological Applications* 9:864-79.
- Trettin, C. C., M. R. Gale, M. F. Jurgensen, and J. W. McLaughlin. 1992. Carbon storage response to harvesting and site preparation in a forested mire in Northern Michigan, USA. *Suo* 43:281-84.
- Trettin, C. C., M. F. Jurgensen, J. W. McLaughlin, and M. R. Gale. 1997. Effects of forest management on wetland functions in a sub-boreal swamp. p. 411-28. *In* C. C. Trettin, M. F. Jurgensen, D. F. Grigal, M. R. Gale, and J. K. Jeglum (eds.) *Northern Forest Wetland Ecology and Management*. CRC Press, Boca Raton, FL, USA.
- Vellak, K. and J. Paal. 1999. Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. *Biology and Conservation* 8: 1595-1620.

Manuscript received 1 June 2006; revisions received 11 October 2006; accepted 22 November 2006.

## Bryophytes

Minimum Cover 0.1%	Cover 0.5%			Cover 1%			Cover 5%			Cover 10%			Cover 25%			Cover 50%								
Species / Microsite	Control			120m, Uncut			30m, Uncut			Harvest Only			Bedded			Trenched			30m, Cut, Trenched			120m, Cut, Trenched		
	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P
<i>Amblystegium serpens</i>																								
<i>Amblystegium varium</i>				●	●																			
<i>Atrichum undulatum</i>																								
<i>Aulecomnium palustre</i>	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Brachythecium</i> sp.																								
<i>Brachythecium curtum</i>																								
<i>Bryum pseudotriquetrum</i>									●	●	●	●	●	●	●	●	●	●					●	●
<i>Bryum</i> spp.									●															
<i>Ceratodon purpureus</i>																								
<i>Dicranum flagellare</i>	●	●																	●	●	●	●	●	●
<i>Dicranella heteromalla</i>																			●	●				
<i>Dicranum montanum</i>																			●	●	●	●	●	●
<i>Dicranum polysetum</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Dicranum scoparium</i>				●	●	●																		
<i>Hypnum lindbergii</i>	●																							
<i>Hylacomium splendens</i>		●	●																					
Lichen	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Leafy Liverworts	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Moss sp. 1									●	●	●								●	●	●	●	●	●
Moss sp. 2						●																		
Moss sp. 3									●	●														
<i>Pellia</i> sp.														●										
<i>Plagiommium</i> spp.										●														
<i>Plagiothecium denticulatum</i>																								
<i>Pleurozium schreberi</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Polytrichum commune</i>	●	●	●							●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Polytrichum juniperinum</i>											●					●			●	●	●	●	●	●
<i>Pohlia lescuriana</i>								●	●				●											
<i>Pohlia nutans</i>				●								●	●						●	●		●	●	●
<i>Pohlia</i> sp.													●	●	●							●	●	●
<i>Sanionia uncinata</i>																								
<i>Sphagnum angustifolium</i>	●	●										●	●					●	●					●
<i>Sphagnum capitifolium</i>	●	●	●															●	●		●			●
<i>Sphagnum compactum</i>			●	●		●	●	●	●					●	●			●	●		●	●	●	●
<i>Sphagnum cuspidatum</i>				●	●	●	●	●	●	●	●	●	●				●	●	●		●	●	●	●
<i>Sphagnum fallax</i>	●		●	●	●	●	●	●	●								●	●						
<i>Sphagnum flexuosum</i>	●	●	●	●			●	●	●				●	●	●									
<i>Sphagnum fuscum</i>	●									●	●				●									
<i>Sphagnum girgensohnii</i>	●	●	●			●								●				●			●	●		●
<i>Sphagnum nitidum</i>		●	●	●		●				●														
<i>Sphagnum quinquetartum</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Sphagnum recurvum</i>	●	●																						
<i>Sphagnum russowii</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Sphagnum</i> spp.																								
<i>Sphagnum squarrosum</i>																				●			●	●
<i>Sphagnum strictum</i>										●	●	●												●
<i>Sphagnum subtile</i>										●	●	●												
<i>Sphagnum subsecundum</i>		●	●							●														
<i>Sphagnum teres</i>									●										●					
<i>Tetraphis pellucida</i>	●								●															

## Appendix 1. Continued.

## Herbaceous

Minimum Cover 0.01%	•	Cover 0.5%	●	Cover 1%	●	Cover 5%	●	Cover 10%	●	Cover 25%	●	Cover 50%	●											
	Control			120m, Uncut			30m, Uncut			Harvest Only			Bedded			Trenched			30m, Cut, Trenched			120m, Cut, Trenched		
Species / Microsite	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P	M	S	P
<i>Botrychium</i> spp.																								
<i>Carex lacustris</i>										●	●													
<i>Carex</i> sp.				●	●	●													●	●		●	●	●
<i>Carex stricta</i>																			●	●	●	●	●	●
<i>Carex viridula</i>		●	●	●	●	●				●	●	●	●	●	●	●	●	●		●	●		●	●
<i>Coptis trifolia</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Deschampsia flexuosa</i>			●		●	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Dryopteris spinulosa</i>																			●	●	●	●	●	●
<i>Epigaea repens</i>																	●	●		●			●	●
<i>Gaultheria hispida</i>																				●	●	●	●	●
<i>Grass</i> sp.							●	●	●		●								●	●	●	●		
<i>Hieracium</i> sp.																								●
<i>Hypericum canadense</i>	●	●				●	●	●	●	●		●	●		●	●	●	●	●	●	●	●	●	●
<i>Iris versicolor</i>											●	●				●			●	●	●	●	●	●
<i>Juncus</i> sp.	●	●												●						●				
<i>Lycopodium obscurum</i>														●	●					●				
<i>Lycopus uniflorus</i>																							●	
<i>Maianthemum canadense</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Melampyrum lineare</i>	●	●	●	●					●	●					●	●		●	●	●	●		●	
<i>Panicum</i> sp.																	●	●						
<i>Pteridium aquilinum</i>																				●				
<i>Rubus hispida</i>										●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Smilacina trifolia</i>														●										
<i>Solidago graminifolia</i>													●		●							●	●	●
<i>Solidago uliginosa</i>																			●	●	●	●	●	●
<i>Trientalis borealis</i>	●		●																●	●		●		
<i>Viola</i> sp.																			●	●	●		●	

## Appendix 1. Continued.

## Woody

[illegible]